Reconstruction of shell patterns using deterministic continuous mathematical models

Brunner, Patrick; patrickbrunner91@gmail.com
Heinze, Lea; heinze.lea@gmx.de

Abstract
Two deterministic reaction-diffusion models are introduced to simulate a general molecular mechanism, which can produce a variety of different pigmentation patterns on the shells of molluscs. We focused on the reconstruction of patterns observed on the surface of shells collected in the Wadden Sea of Northern Germany, which include horizontal and vertical stripes, as well as oblique lines and dots. The patterns were analyzed in respect to their parameter sensitivity and varying initial conditions. We show that the models have high potential to reproduce very different patterns with only modest changes in the parameters. Such theoretical approaches can be used to understand the mechanisms involved in pigmentation.

Introduction

Certain molluscan taxa are able to form a wide variety of patterns on their shells. These patterns can either be formed by different pigmentation or by an alternating thickness of the shell. Those traits are achieved by secretion of molecules such as proteins along the growth-line of the mantle (Weiner & Traub, 1984). The biological use of pigmentation patterns has not been fully understood, if there is any. Some animals which form very vivid colors on their shells live burrowed in the sand or are only active at night. While it is not clear what use those colors might have, the different thicknesses which lead to a relief-like structure on the shell can for example increase friction on the sand while burrowing (Seilacher, 1972).

Since only the mantle cells form the shell, the whole shell can be understood as a time-space-plot of the secretion of pigments. While the space reflects the activity of each mantle cell during the formation of the shell, the time can be understood as the growing cycles of the shell.

Several attempts to model those activities have been made (Meinhardt & Klingler, 1987); Madzvamuse et al., 2001) using a reaction-diffusion mechanism. We sought to investigate the use of those very general and simplified models and reproduce the patterns shown by Meinhardt & Klingler (1987) using numerical solutions to the presented partial differential equations.

Furthermore we compare the theoratically constructed patterns with those found in real shells collected from the shore in List (Germany) to validate the model.

Material and Methods

Shell collection

Shells were collected in the Wadden Sea of Sylt, on the beach in front of the Alfred Wegener Institute (AWI) in List between the 6th and 8th of October 2017. Shells were collected without distinguishing between mud or sand flats and only in regards to their shell patterns. Shells of mussels and snails have been collected with no respect to their taxa but only based on their colored shell pattern. 11 different species could be collected and identified (see Table 1 in Supplemental Material). Observed patterns include horizontal and vertical stripes, oblique lines, dots or any combination of those features. It should be mentioned that the same taxon can have varying patterns or colors. These representative patterns are used to be compared to the modelled patterns.

Mathematical model

To comprehend the molecular principles guiding pattern formation during shell growth, we used a published model of Meinhardt & Klingler (1987). The author proposed two slightly different mechanisms which are thought to explain the most common patterns on mussel and snail shells. Both models are

reaction-diffusion models, meaning that the system is characterized by two compounds whose concentration is influenced by their diffusion and biochemical reactions with at least one compound coloring the shell surface. Therefore, the concentration of the compounds a and b depend on their spatial position and the time point of measurement: a(x,t), b(x,t). Knowledge of these functions would fully explain the observed shell pattern.

To formulate the functions a(x,t) and b(x,t), the model uses partial differential equations (pde). Such formalisms are used when the functions of interest, a(x,t) and b(x,t), are unknown, but an explicit formulation of the derivative of a and b can be found. By solving the equation which describes the derivative of a and b, the functions a(x,t) and b(x,t) can be found.
The following pde describes the activator-substrate model, published by Meinhardt & Klingler (1987).

$$\frac{\partial a}{\partial t} = \rho s a^* - \mu a + D_a \frac{\partial^2 a}{\partial x^2}$$

$$\frac{\partial s}{\partial t} = \sigma - \rho s a^* - \upsilon s + D_s \frac{\partial^2 s}{\partial x^2}$$

In these pde, the temporal change of activator a and substrate s depend both on their spatial diffusion, described by the diffusion constants D_a and D_s. Furthermore, both substances are decayed, which is influenced by their decay rate μ and υ, and the substrate s is produced with rate σ. Additionally, a increases due to its autocatalytic reaction a*, which is defined by:

$$a^* = \frac{a^2}{1 + a^2 \kappa} + \rho_0$$

In this, $\varkappa$ limits the influence of autocatalysis to a value of $a^* \approx \varrho_0$ if $\varkappa$ is very high. ϱ_0 is a value for the production rate of the activator. In general, the factor ϱ determines the influence of the autocatalysis on the change of a. The model also describes, that substrate s is needed for autocatalysis and at the same time consumed during this process.
In contrast to that, the activator-inhibitor model, also published by Meinhardt & Klingler (1987), is defined in the follow

$$\frac{\partial a}{\partial t} = \frac{\rho a^*}{h} - \mu a + D_a \frac{\partial^2 a}{\partial x^2}$$

$$\frac{\partial h}{\partial t} = \sigma + \rho a^* - \upsilon h + D_h \frac{\partial^2 h}{\partial x^2}$$

It can be easily seen that these equations are nearly equal to the activator-substrate model, with the same diffusion constants D_a and D_h, decay rates μ and υ, constant inhibitor production σ, autocatalysis a*, and the factor ϱ determining the influence of the autocatalysis. The only difference between the two description systems is the inhibiting influence of h on the autocatalytic productivity of a. Additionally, h is not being consumed during autocatalysis but produced instead which means that h inhibits its own self-producing process.
In these models, the activator is assumed to be the coloring agent, the concentration of which has to be determined. For that, we solve the pde numerically by fixing the initial concentrations a(x, 0) and s(x, 0) or h(x, 0) and assuming discrete space and time steps, for which $\partial a/\partial t \approx \Delta a = a(t_{n+1}) - a(t_n)$. In this way, we can calculate the concentration of a substance at a certain point in time and space easily by simply tracing it bac $a(x_n, t_n) = a(x, t_{n-1}) + \Delta a$

To find ideal parameters to reproduce the patterns observed in real molluscan shells collected from the shores of the Wadden Sea in List (Sylt), we first repeated the results of Meinhardt & Klingler (1987) with the parameter values found in this publication and used this as a starting point for further parameter adjustments.
We used the programming language Python2.7 for solving the calculations and plotting the solutions.

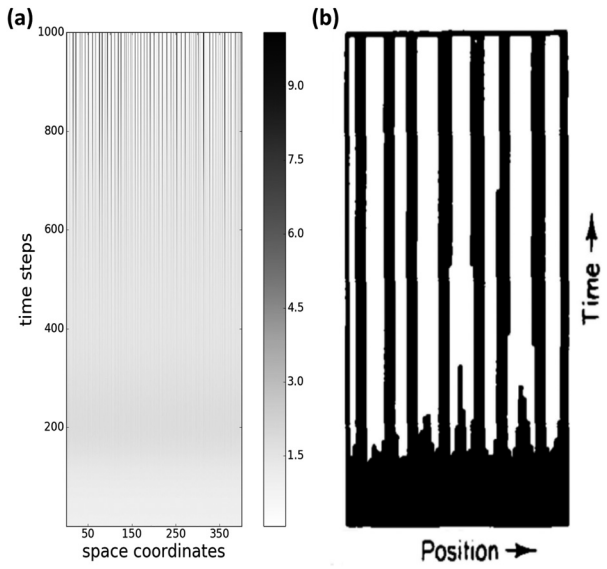

Fig. 1. Simulation of vertical stripes with the activator-substrate model. (a) implemented model, calculated with $\varkappa$=0, ϱ= 0.01 ± 1%, ϱ_0=0.001 , σ=0.015, D_a=0.002, D_s=0.4, ν=0, μ=0.01 and uniform initial conditions (b) results of Meinhardt & Klingler (1987).

Results

Pattern modelling

We focused on the found patterns without considering shell geometry or different growing rates linked to tides or seasons. It should be mentioned that comparison to the results of Meinhardt & Klingler (1987) is inaccurate due to missing time and space scales, so that the influence of misleading visualization effects while comparing cannot be avoided.

Vertical stripes

Vertical stripes evolve due to an oscillation of the pigment concentration in space while being stable in time. This means that pigment production of all cells is constant with certain cells producing pigment all the time. The activator-substrate model used the same parameters of Meinhardt & Klingler (1987) to reproduce stripes perpendicular to the growing edge of the shell. Figure 1 compares the results of Meinhardt & Klingler (1987) with the outcomes of the present study which sets the initial conditions of activator and substrate concentrations to 1 at all points in space. Obviously, vertical stripes could be reproduced in these model settings despite an initial spatial homogeneity. Nevertheless, the reproduced pattern never shows lines broader than a few cells. Variation of parameters, such as diffusion constants, does not change this feature. To evaluate the stability of reconstructed patterns, all parameters have been varied separately by holding the remaining parameters constant. It can be seen that parameters in general have the potential to amplify or fade the pattern (see Supplemental Material, Figures 2-3).

The activator-inhibitor model has first been tested by using the same parameters as Meinhardt & Klingler (1987) to reproduce vertical stripes. As Meinhardt & Klingler (1987) insert cells at given intervals in time, the initial conditions were chosen not to be spatially uniform but to have four initially activator producing cells. As seen in Figure 2, the used model does not account for the triangular shell growth, but was able to produce vertical stripes which are very stable in time. Furthermore, using very different parameters enables the model to form broad stripes even when using uniform initial conditions analog to the activator-substrate model, so that no spatial heterogeneity had to be assumed externally (see Figure 2). The broad width of the stripes differs remarkably from the activator-substrate model, for which no parameters could be found to produce stripes of similar breadth. Both models, however produce very similar patterns on smaller time scales (see Supplemental Material, Figure 1), so they only differ in their long-term behavior. General, it is observed that these vertical patterns are sensitive to only some parameter changes (see Supplemental Material, Figure 4-5).

Horizontal stripes

To reproduce horizontal lines which are parallel to the growing edge, the pigment concentration has to oscillate in time with equal concentration of activator in space for each time point. Therefore, no spatial gradient between cells exists and diffusion is not a critical parameter for this pattern.

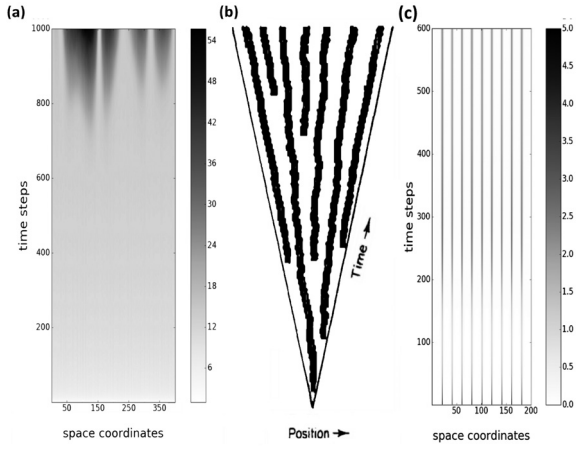

Fig. 2. Simulation of vertical stripes with the activator-inhibitor model. (a) implemented model, calculated with $\varkappa$=0 (0.15), ϱ= 0.2 ± 25% (2.5%), ϱ_0=0.01 , σ=0.01 (not given), D_a=0.01, D_h=0.495 (0.4), ν=0.02, μ=0.02 and uniform initial conditions (b) results of Meinhardt & Klingler (1987) (c) implemented model, calculated with $\varkappa$=0.15, ϱ= 0.2 ± 2.5%, ϱ_0=0.01 , σ=0.0025 (not given), D_a=0.01, D_h=0.4, ν=0.2, μ=0.2 and four initial activator producing cells. For parameters differing from Meinhardt & Klingler (1987), Meinhardt's parameter values are given in brackets.

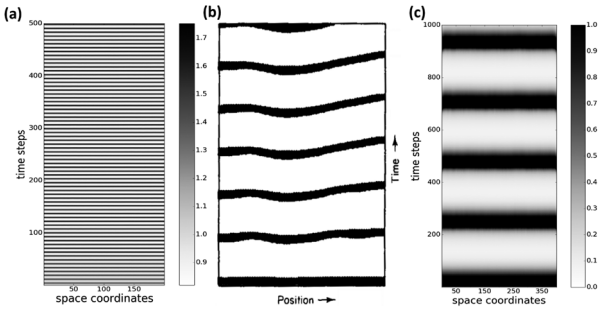

Fig. 3. Simulation of horizontal stripes with the activator-substrate and activator-inhibitor model. (a) activator-substrate model, calculated with $\varkappa$=0.1, ϱ= 0.9, ϱ_0=0.001, σ=0.9, D_a=0.05, D_s=0.03, ν=0.11, μ=0.7 and uniform initial conditions (b) results of Meinhardt & Klingler (1987) using the activator-inhibitor model (c) activator-inhibitor model, calculated with $\varkappa$=0.0004, ϱ= 0.1 (0.05) ± 7.5%, ϱ_0=0.02 , σ=0.0075, D_a=0.1, D_h=0, ν=0.03, μ=0.05 and uniform initial conditions. For parameters differing from Meinhardt & Klingler (1987), Meinhardt's parameter values are given in brackets.

When using the activator-substrate model, no parameters are given from Meinhardt & Klingler (1987) to produce such a pattern, so a new set of parameters has been determined. This resulted in a strong horizontal oscillation of the activator with a relatively short periodicity when using uniform initial conditions. Figure 3 compares the reproduced pattern with the results of Meinhardt & Klingler (1987) using the activator-inhibitor model. It can be seen, that the modelling results differ in their temporal scale and their curviness which is not surprising as the parameters used for these models differ dramatically. Nevertheless, the reproduced horizontal stripes appeared to be relatively robust to parameter fluctuations and do not change on very long time scales (see Supplemental Material, Figures 6-7).

Given the parameters of Meinhardt & Klingler (1987) with only small changes to ϱ and uniform initial conditions, the activator-inhibitor model was able to produce horizontal stripes as expected. Displayed in Figure 3, the oscillation shows a remarkably longer periodicity compared to the activator-substrate model which seems to be in a similar range of Meinhardt & Klingler (1987). Nevertheless, the bending observed by Meinhardt & Klingler (1987, see Figure 3b) could not be reproduced. Nevertheless, the horizontal oscillation is also observed to show a higher robustness to parameter fluctuations (see Supplemental Material, Figures 8-9).

Oblique lines and dots

Only the activator-inhibitor model was used to model oblique lines and dots. To form these patterns, the model itself has to be changed: instead of holding all parameters constant during one simulation, the production of the activator, ϱ_o, has to follow a sinusoidal oscillation in time but remains constant in space. As the shape of the oscillation was not mentioned by Meinhardt & Klingler (1987), ϱ_o has been chosen in the following way:

$\varrho_o = 0.008 * \sin((\pi * t)/135)$

Additionally, stronger noise was introduced in testing the parameters ϱ and D_a. $\varkappa$ and ϱ differ in their values from the given parameters. All other parameters are identical to the ones given by Meinhardt & Klingler (1987) whose results are compared to the reconstructed patterns in Figure 4. It can be seen that oblique lines of the model are more distinct and show a higher spatial fluctuation. Furthermore, the oblique lines do not show a reproducible spatial periodicity as the one observed in the Meinhardt & Klingler (1987) results.

To obtain dots, the parameter values of D_a, D_h, $\varkappa$, ϱ and the variation of ϱ have to be adjusted and differ from the parameter set given by Meinhardt & Klingler (1987). Additionally, the oscillation of ϱ_o had to change to a much higher periodicity so that dots can be clearly separated and do not merge to continuous lines:

$\varrho_o = 0.2 * \sin((\pi * t)/10)$

Similar to the results of Meinhardt & Klingler (1987) the shapes of the dots are stretched along the temporal axis but are clearly distinguishable (see Figure 5). Furthermore, the model needs a very long time interval until the dots are created, so that considerably fewer dots are visible in the resulting plot.

Biological patterns

Shell patterns of collected molluscs include horizontal stripes, for example shown by *Spisula elliptica* and *Macoma baltica*, vertical lines, which can be seen at some *Crassostrea gigas* and *Cerastoderma edule*, and dots, shown by almost all *Crepidula fornicata*. Sometimes, also a combination of patterns can be

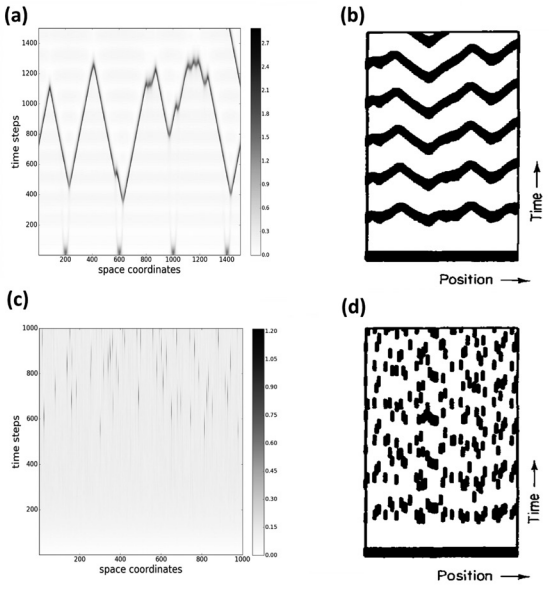

Fig. 4. Simulation of oblique lines and dots with the activator-inhibitor model. (a) implemented model, calculated with $\varkappa$=0 (0.0004), ϱ= 0.1 (0.05)) ± 17.5% (15%), ϱ_0=0.008 (0.2) with sinoidal oscillation , σ=0.0075, D_a=0.15 (0.1), D_h=0, ν=0.03, μ=0.05 and four initial activator producing cells. (b) results of oblique lines by Meinhardt & Klingler (1987) (c) activator-inhibitor model, calculated with $\varkappa$=0.0001 (0.0004), ϱ= 0.068 (0.05) ± 50% (15%), ϱ_0= 0.2 with sinoidal oscillation, σ=0.0075, D_a=0 (0.1), D_h=0.004 (0), ν=0.03, μ=0.05 and uniform initial conditions. (d) results of dot simulations by Meinhardt & Klingler (1987). For parameters differing from Meinhardt & Klingler (1987), Meinhardt's parameter values are given in brackets.

observed, for example most *Crepidula fornicata* show a combination of dots and vertical lines.

Direct comparison between modelling results and biological patterns shows that the general pattern can be conserved. Nevertheless, biological patterns show much more variability within a shell and in comparison between individuals.

Discussion

The goal of this study was the theoretical reconstruction of shell patterns found on molluscs shells collected in the Northern Wadden Sea of Germany. The reconstruction of shell patterns was successful if one focuses on the generalized patterns found on sea shells such as vertical and horizontal lines as well as dots. Oblique lines, which are also known to appear on shell patterns such as on Liochoncha spec (van der Meij et al., 2010), could also be created by a model. Nevertheless, there are differences between modelling outcomes and biological structures: the modelling results were not able to depict the same richness of pattern variability and combination of different patterns, which is likely to be caused by a lack of noise in the parameter values. Further studies would be needed to investigate this hypothesis. Furthermore, the model's behavior could indicate that mixed patterns might arise when parameters are allowed to vary in time and space, but checking this hypothesis is beyond the scope of this analysis. The models were able to reproduce a variety of patterns only due to some parameter variation. This shows the high potential of the model to explain many patterns shown in nature using a relatively simple system. However, observed similarities between modelling results and biological patterns can never proof but only indicate that the assumed system can be used by the organisms to produce its patterns.

Two different models have been used to reconstruct biological patterns. These models both use an activator-antagonist approach. While the first model uses substrate as an antagonist which is necessary for the activator production and is also decayed during this process, the second uses an inhibitor that represses the activator production while being produced. Despite this strong mechanistic difference, both models were able to reproduce vertical and horizontal stripes, but under very different parameter conditions. These differences could explain why some essential properties of the patterns such as line width and periodicity are not conserved between these models. As the biological system is not able to freely choose parameter values but is limited by the surrounded physical conditions, the findings might suggest that a different mechanism can be chosen depending on the surrounding conditions. Therefore, the models show similar outcomes but can be applied in different biological situations. So, the statement by Meinhardt & Klingler (1987) that both models cannot be distinguished only by the outcome cannot be confirmed. Additionally, other differences between the model outcomes and the results of Meinhardt & Klingler (1987) can be observed: some patterns such as oblique lines and dots can only be reproduced with parameters which strongly differ from the given ones. Especially the noise on parameter ϱ had to increase to form the patterns of interest which could indicate that Meinhardt & Klingler (1987) used longer time scales for their simulation. But as the plots of Meinhardt & Klingler (1987) do not show a legend in space and in time pattern properties such as the time length of an oscillation cannot be reasonably compared. The reproduction of results depicted by Meinhardt & Klingler (1987) was also hindered as no initial conditions were given by Meinhardt & Klingler (1987) but strong effects of initial conditions in the final modelling outcome have been observed. So in summary, only similarities between the reconstructed patterns and the results of Meinhardt & Klingler (1987) can be observed but no qualitative conclusion can be drawn.

In general, it was not possible to analyze all possible parameter variations and therefore to be able to fully understand and evaluate the potential of both models to show all their possible patterns. This analysis would be much deeper and more time consuming. Furthermore, the models have not been inspired by known molecular mechanisms who guide pattern formation in shells. For example, pattern formation is reported to depend on the genetic information of the expressing cells (Luttikhuizen & Drent, 2008), so that patterns can be caused by epigenetic variations over time, leading to different expression rates of secreted proteins (Jackson et al., 2006). In the used models, the epigenetic background is not considered to influence the expression, but despite constant expression rate the concentrations are able to form patterns due to diffusion and reaction effects. A very different approach to model more closely on the biological system is to directly simulate the neural activity guiding the pattern forming process (Boettiger et al., 2009). Such approaches might prove useful in the future to get more insights into the molecular system.

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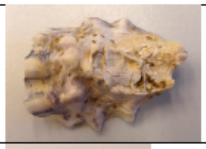
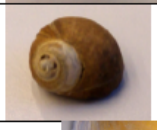
Supplemental Material

Table 1: List of collected shells of mussels and snails between the 6th and 8th of October 2017 at Wadden Sea of Sylt, Germany

Species	Representative shell pattern
Ostrea edulis	
Spisula elliptica/solida	
Ensis ensis/silica	
Crassostrea gigas	
Littorina littorea	
Lutraria lutraria	
Turritella communis	
Buccinum undatum	
Crepidula fornicata	

Cerastoderma edule	
Mytilus edulis	

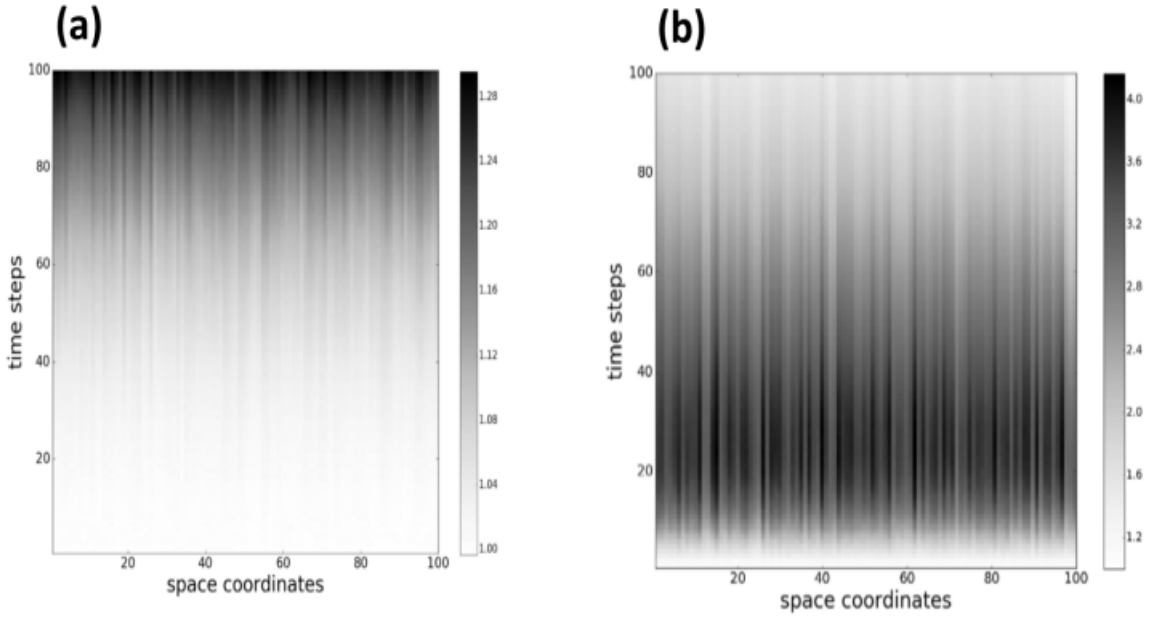


Figure 1: Simulation of vertical stripes. (a) activator-substrate model, calculated with $\boldsymbol{\kappa = 0}$, $\boldsymbol{\rho} = 0.01 \pm \mathbf{1\%}$, $\boldsymbol{\rho_0 = 0.001}$, $\boldsymbol{\sigma = 0.015}$, $\boldsymbol{D_a = 0.002}$, $\boldsymbol{D_s = 0.4}$, $\boldsymbol{\nu = 0}$, $\boldsymbol{\mu = 0.01}$ and uniform initial conditions. (b) activator-inhibitor model, calculated with $\boldsymbol{\kappa = 0}$ (0.15), $\boldsymbol{\rho} = 0.2 \pm \mathbf{25\%}$ (2.5%), $\boldsymbol{\rho_0 = 0.01}$, $\boldsymbol{\sigma = 0.01}$ (not given), $\boldsymbol{D_a = 0.01}$, $\boldsymbol{D_h = 0.495}$ $(\mathbf{0.4})$, $\boldsymbol{\nu = 0.02}$, $\boldsymbol{\mu = 0.02}$ and uniform initial conditions. Both models show similar stripe pattern for short time scales.

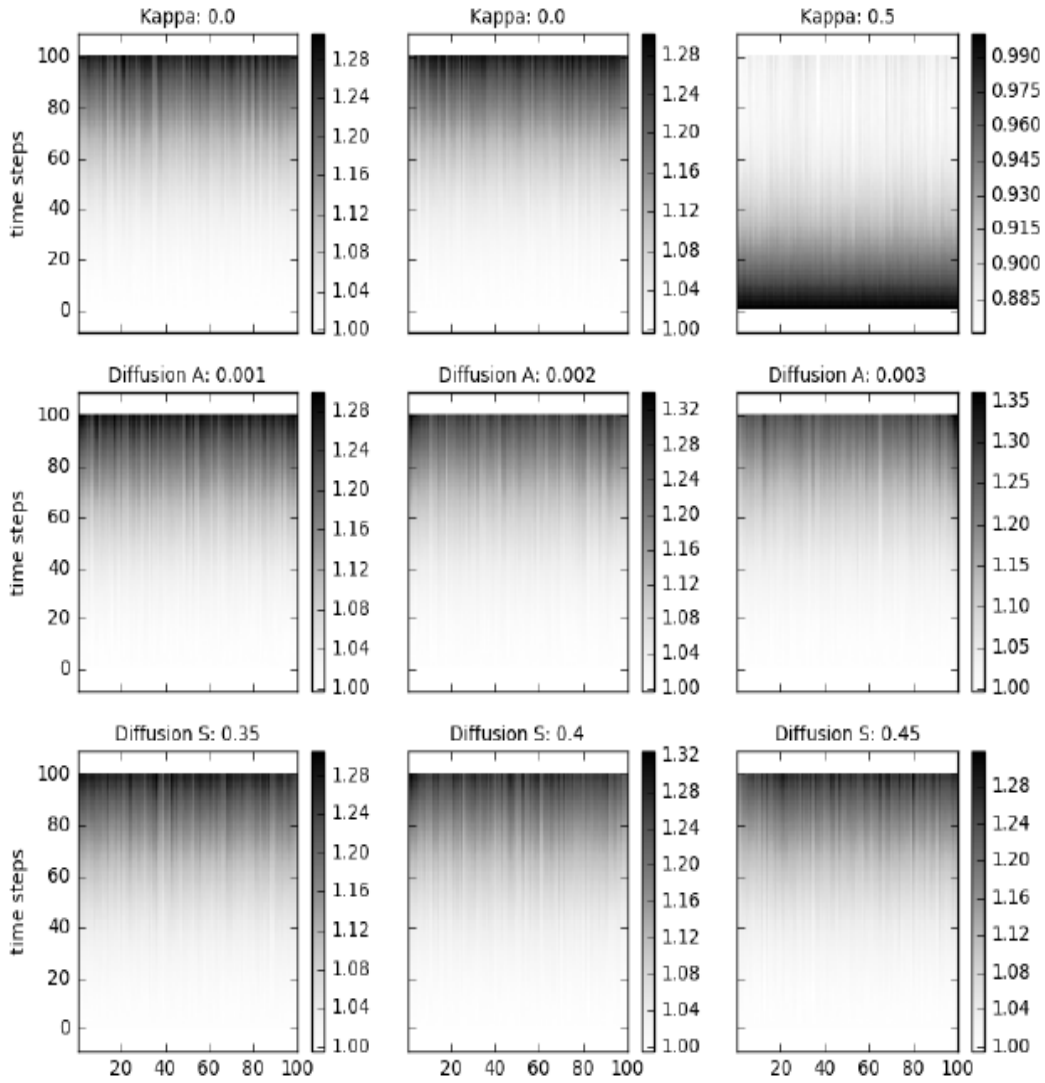


Figure 2: Sensitivity of vertical stripes simulated with activator-substance model to parameter variations. Each row varies a different parameter by holding the other parameters constant. All pictures in middle column are constructed using the default parameter set. Default parameters: $\boldsymbol{\kappa = 0}$, $\boldsymbol{\rho} = 0.01 \pm \mathbf{1\%}$, $\boldsymbol{\rho_0 = 0.001}$, $\boldsymbol{\sigma = 0.015}$, $\boldsymbol{D_a = 0.002}$, $\boldsymbol{D_s = 0.4}$, $\boldsymbol{\nu = 0}$, $\boldsymbol{\mu = 0.01}$ and uniform initial conditions

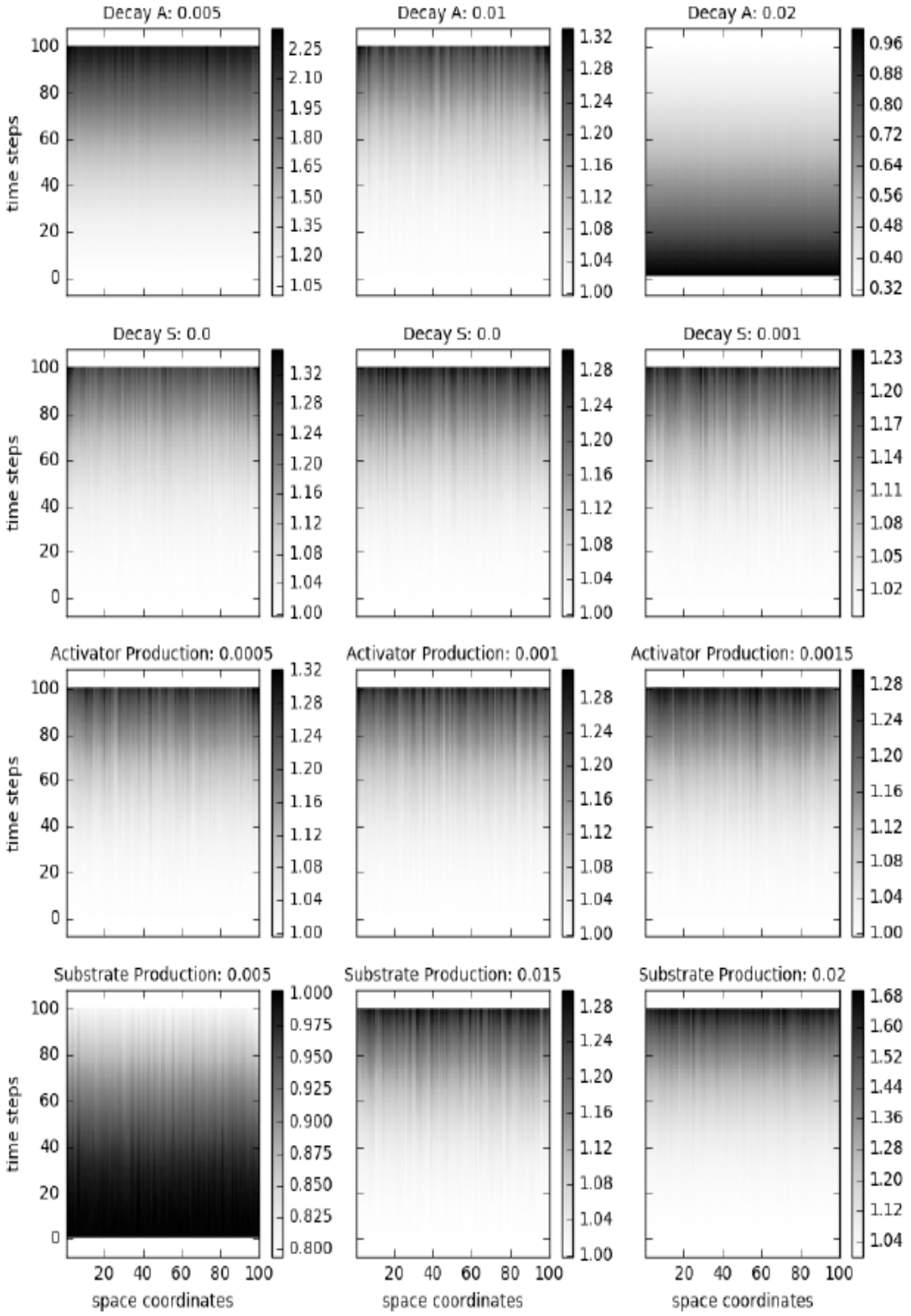


Figure 3: Sensitivity of vertical stripes simulated with activator-substance model to parameter variations. Each row varies a different parameter by holding the other parameters constant. All pictures in middle column are constructed using the default parameter set. Default parameters: $\boldsymbol{\kappa = 0}$, $\boldsymbol{\rho = 0.01 \pm 1\%}$, $\boldsymbol{\rho_0 = 0.001}$, $\boldsymbol{\sigma = 0.015}$, $\boldsymbol{D_a = 0.002}$, $\boldsymbol{D_s = 0.4}$, $\boldsymbol{\nu = 0}$, $\boldsymbol{\mu = 0.01}$ and uniform initial conditions

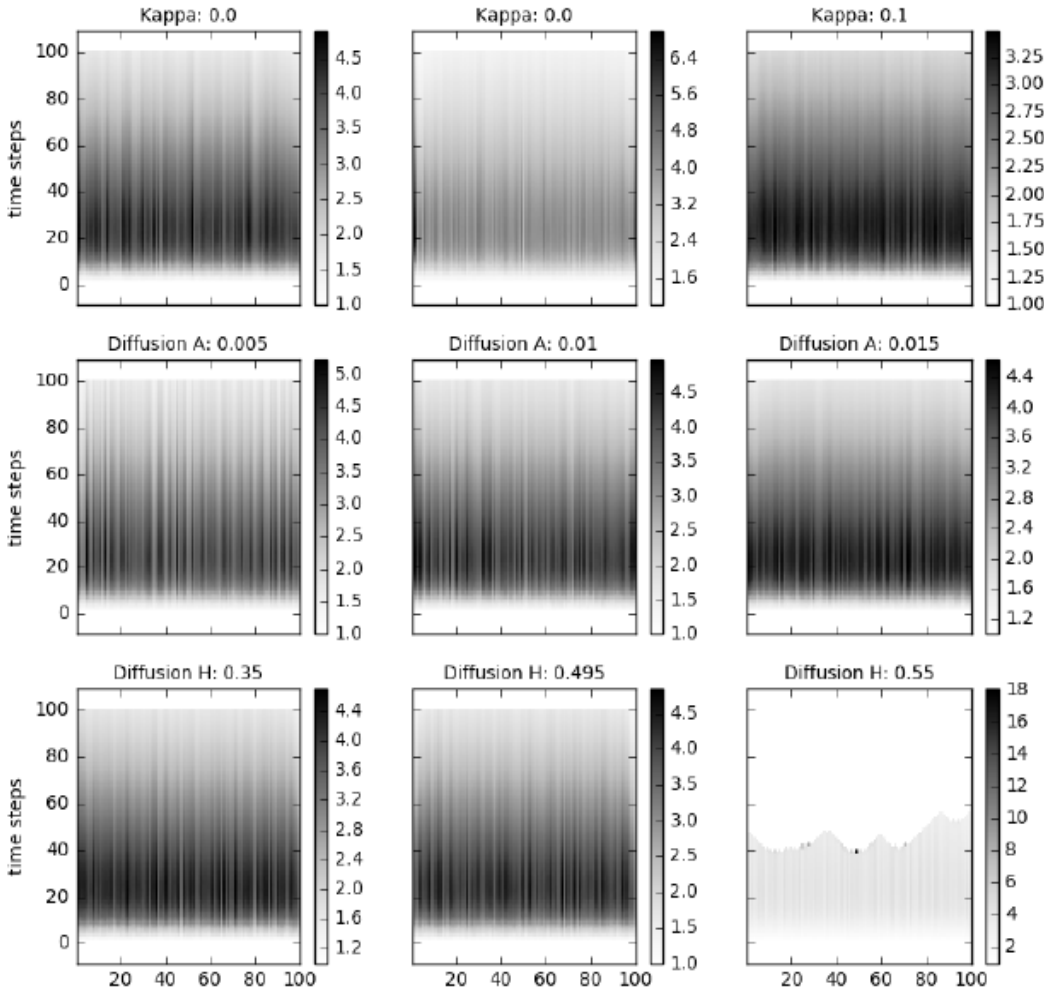


Figure 4: Sensitivity of vertical stripes simulated with activator-inhibitor model to parameter variations. Each row v
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$\boldsymbol{\mu = 0.02}$ and uniform initial conditions

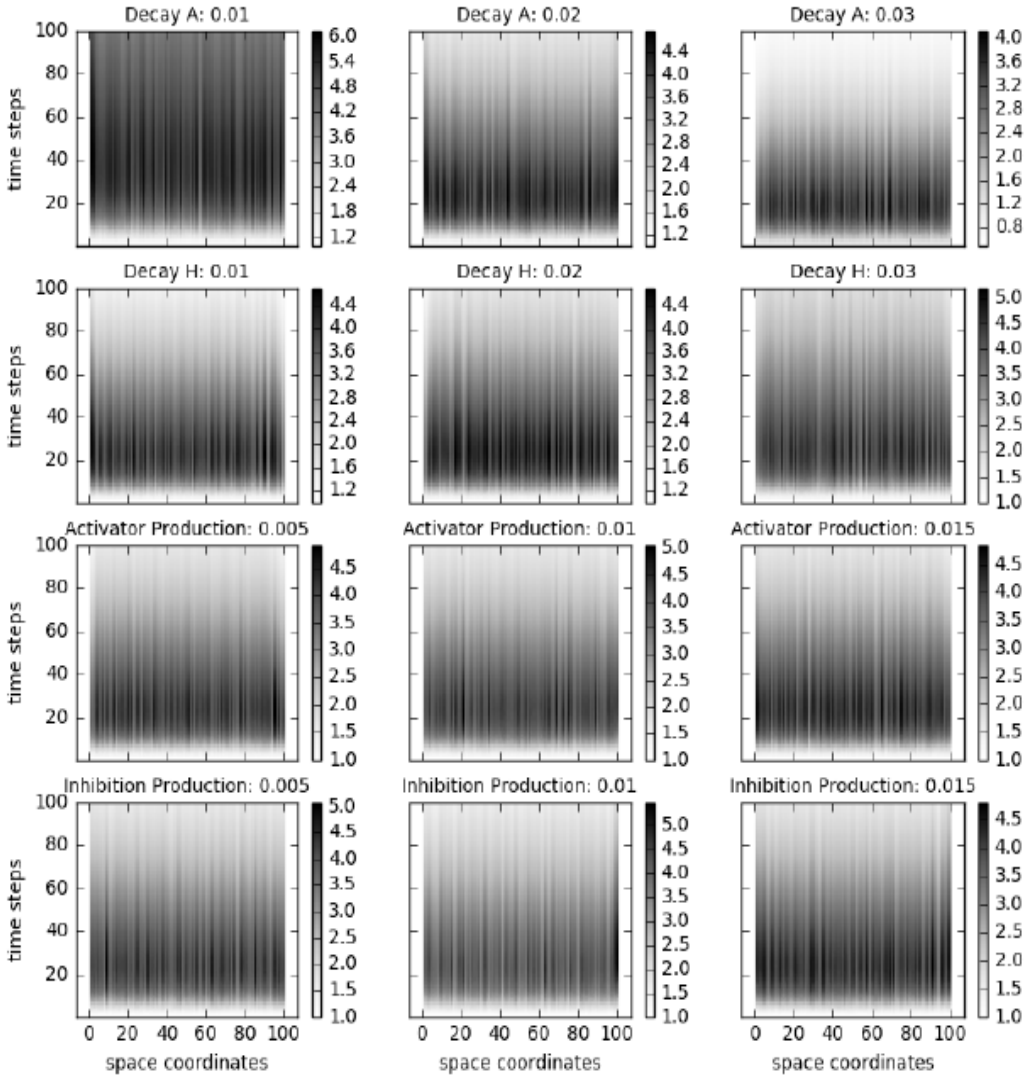

Figure 5: Sensitivity of vertical stripes simulated with activator-inhibitor model to parameter variations. Each row varies a different parameter by holding the other parameters constant. All pictures in middle column are constructed using the default parameter set. Default parameters: $\boldsymbol{\kappa = 0}$, $\boldsymbol{\rho} = 0.2 \pm \mathbf{25\%}$, $\boldsymbol{\rho_0 = 0.01}$, $\boldsymbol{\sigma = 0.01}$, $\boldsymbol{D_a = 0.01}$, $\boldsymbol{D_h = 0.495}$, $\boldsymbol{\nu = 0.02}$, $\boldsymbol{\mu = 0.02}$ and uniform initial conditions

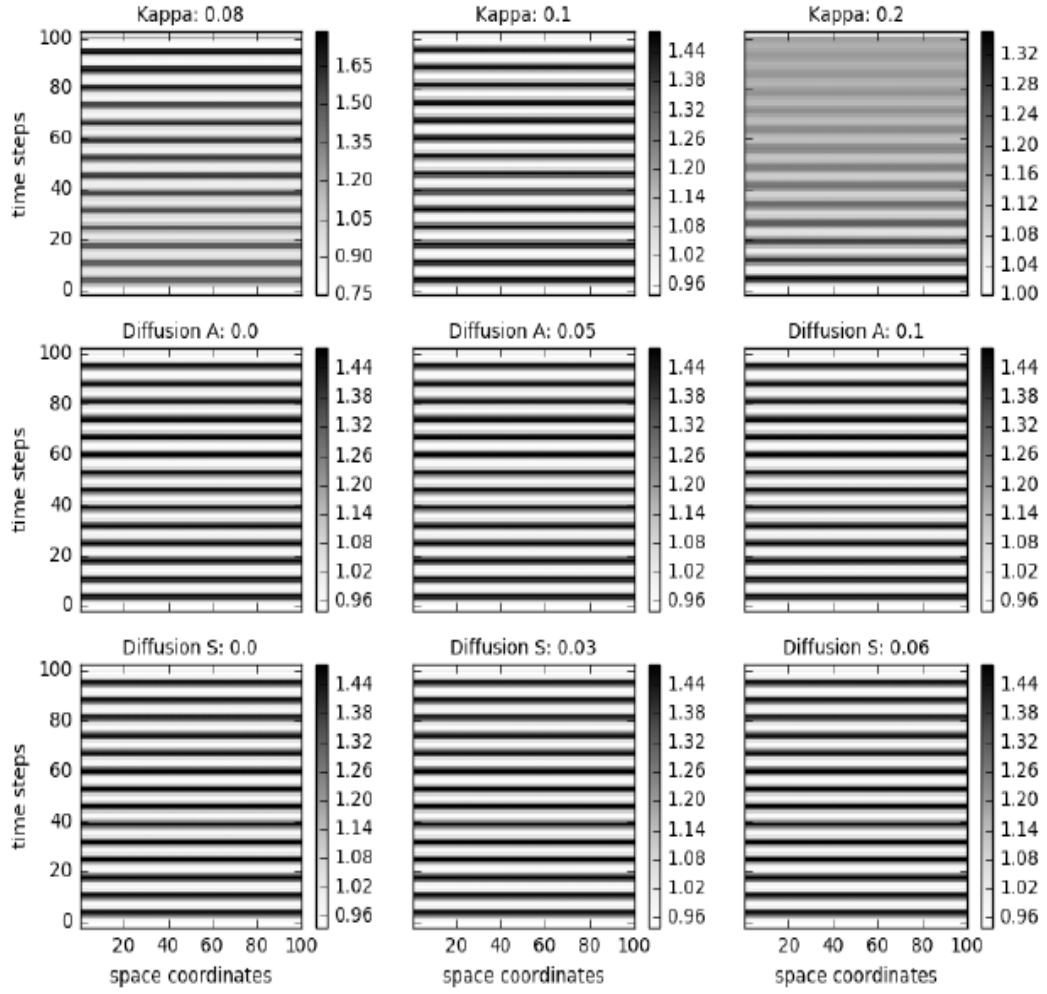

Figure 6: Sensitivity of horizontal stripes simulated with activator-substance model to parameter variations. Each row varies a different parameter by holding the other parameters constant. All pictures in middle column are constructed using the default parameter set. Default parameters: **with** $\kappa = 0.1$, $\rho = 0.9, \rho_0 = 0.001, \sigma = 0.9, D_a = 0.05, D_s = 0.03$, $\nu = 0.11$, $\mu = 0.7$ and uniform initial conditions

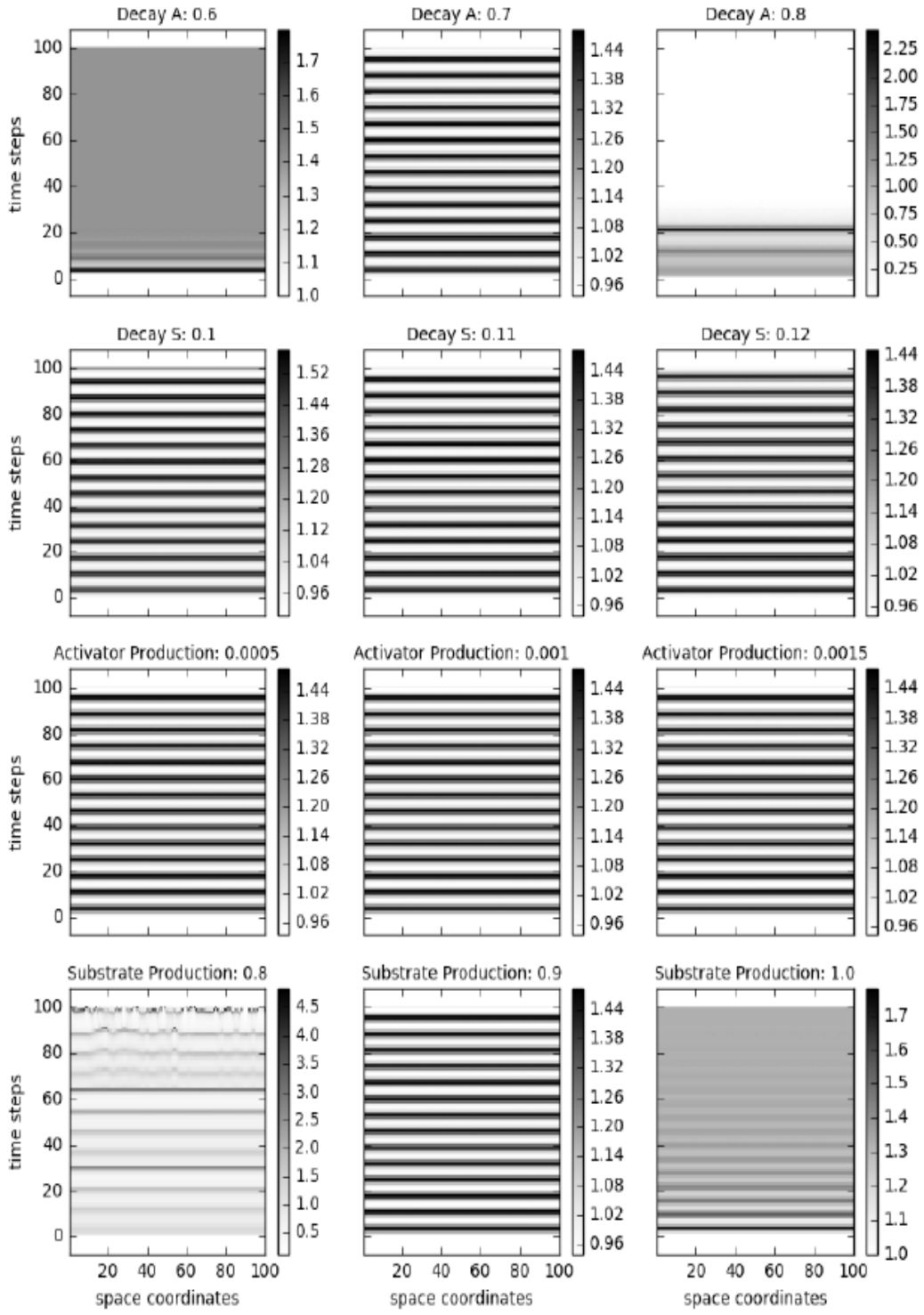

Figure 7: Sensitivity of horizontal stripes simulated with activator-substance model to parameter variations. Each row varies a different parameter by holding the other parameters constant. All pictures in middle column are constructed using the default parameter set. Default parameters: **with** $\kappa = 0.1$, $\rho = 0.9, \rho_0 = 0.001, \sigma = 0.9, D_a = 0.05, D_s = 0.03$, $\nu = 0.11$, $\mu = 0.7$ and uniform initial conditions

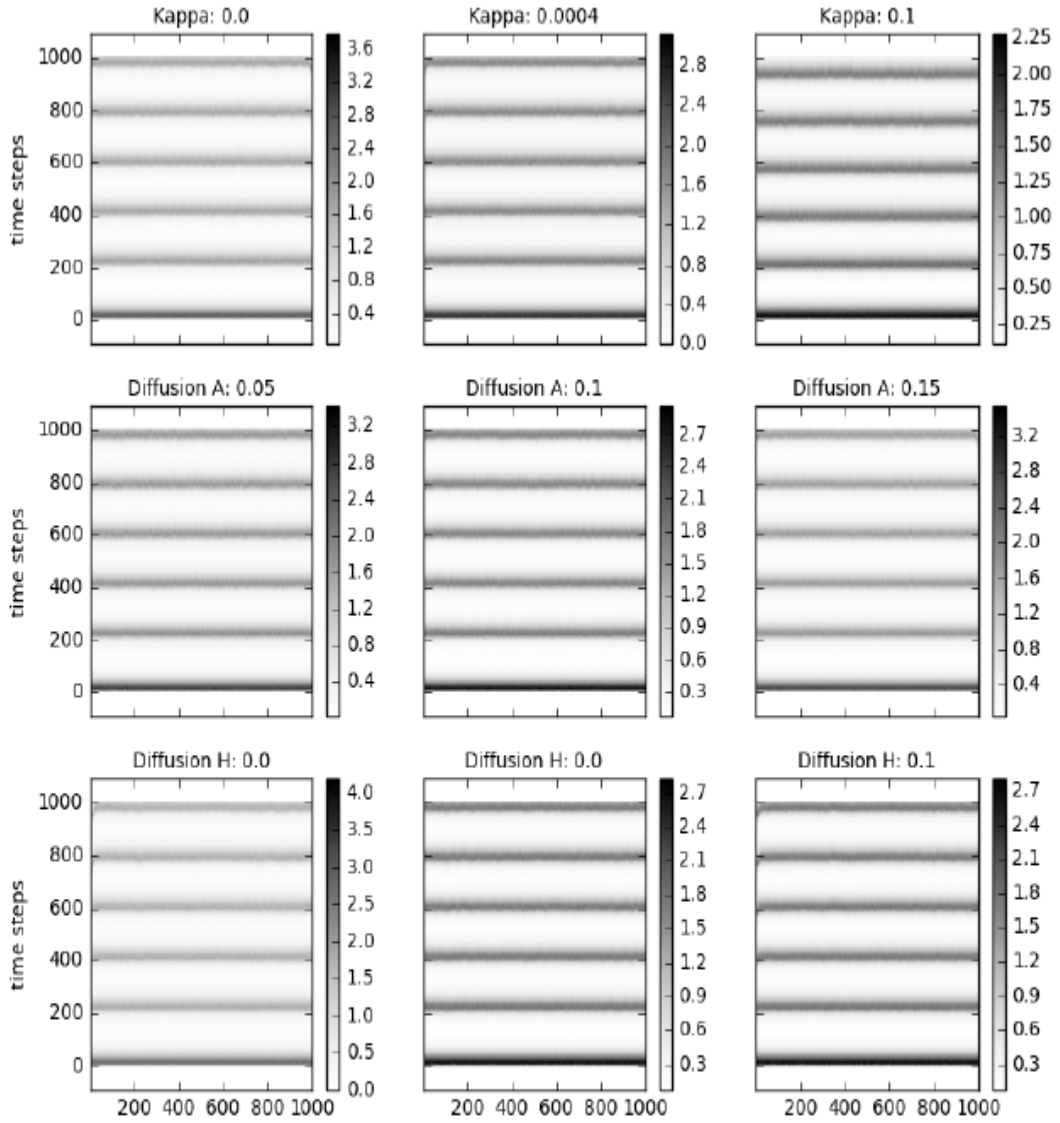

Figure 8: Sensitivity of horizontal stripes simulated with activator-inhibitor model to parameter variations. Each row varies a different parameter by holding the other parameters constant. All pictures in middle column are constructed using the default parameter set. Default parameters: $\boldsymbol{\kappa = 0}.0004$, $\boldsymbol{\rho} = 0.1 \pm \mathbf{7.5\%}$, $\boldsymbol{\rho_0 = 0.02}$, $\boldsymbol{\sigma = 0.0075}$, $\boldsymbol{D_a = 0.1}$, $\boldsymbol{D_h = 0}$, $\boldsymbol{\nu} = 0.03$, $\boldsymbol{\mu = 0.05}$ and uniform initial conditions

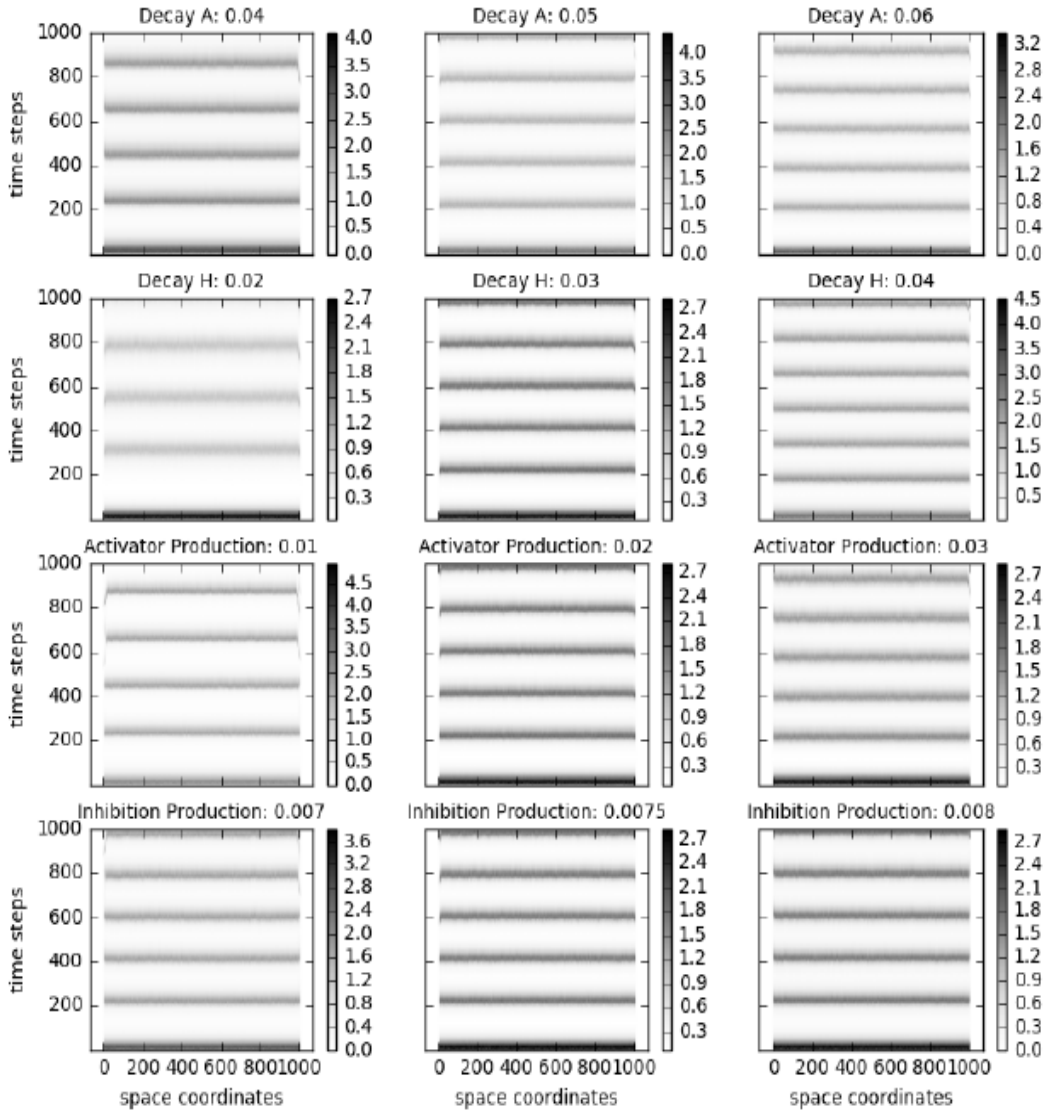

Figure 9: Sensitivity of horizontal stripes simulated with activator-inhibitor model to parameter variations. Each row varies a different parameter by holding the other parameters constant. All pictures in middle column are constructed using the default parameter set. Default parameters: $\boldsymbol{\kappa = 0.0004}$, $\boldsymbol{\rho = 0.1 \pm 7.5\%}$, $\boldsymbol{\rho_0 = 0.02}$, $\boldsymbol{\sigma = 0.0075}$, $\boldsymbol{D_a = 0.1}$, $\boldsymbol{D_h = 0}$, $\boldsymbol{\nu = 0.03}$, $\boldsymbol{\mu = 0.05}$ and uniform initial conditions